100 YEARS Journal of Ecology

British Ecological Society

Journal of Ecology 2014, **102**, 1451–1461 doi: 10.1111/1365-2745.12318

Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants

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Summary

1. Understanding the processes underlying the transition from introduction to naturalization and spread is an important goal of invasion ecology. Release from pests and pathogens in association with capacity for rapid growth is thought to confer an advantage for species in novel regions.

2. We assessed leaf herbivory and leaf-level traits associated with growth strategy in the native and exotic ranges of 13 invasive plant species from 256 populations. Species were native to either the Western Cape region of South Africa, south-western Australia or south-eastern Australia and had been introduced to at least one of the other regions or to New Zealand. We tested for evidence of herbivore release and shifts in leaf traits between native and exotic ranges of the 13 species.

3. Across all species, leaf herbivory, specific leaf area and leaf area were significantly different between native and exotic ranges while there were no significant differences across the 13 species found for leaf mass, assimilation rate, dark respiration or foliar nitrogen.

4. Analysis at the species- and region-level showed that eight out of 13 species had reduced leaf herbivory in at least one exotic region compared to its native range.

5. Six out of 13 species had significantly larger specific leaf area (SLA) in at least one exotic range region and five of those six species experienced reduced leaf herbivory. Increases in SLA were underpinned by increases in leaf area rather than reductions in leaf mass.

6. No species showed differences in the direction of trait shifts from the native range between different exotic regions. This suggests that the driver of selection on these traits in the exotic range is consistent across regions and hence is most likely to be associated with factors linked with introduction to a novel environment, such as release from leaf herbivory, rather than with particular environmental conditions.

7. *Synthesis*. These results provide evidence that introduction of a plant species into a novel environment commonly results in a reduction in the top-down constraint imposed by herbivores on growth, allowing plants to shift towards a faster growth strategy which may result in an increase in population size and spread and consequently to invasive success.

Key-words: assimilation rate, biological invasions, enemy release, herbivory, introduced range, invasion ecology, leaf economic spectrum, native range, specific leaf area

Introduction

Invasion of ecosystems by exotic plants is considered to be one of the main threats to biodiversity globally (Cronk & Fuller 1995; McGeoch *et al.* 2010; Vila *et al.*, 2011), with the extinction debt created by invasive exotic species increasingly being recognized (Gilbert & Levine 2013). Considerable international research effort has been devoted to identifying traits of successful invasive plants (Rejmanek & Richardson 1996; Smith & Knapp 2001; Pyšek & Richardson 2007; Van Kleunen, Weber & Fischer 2010; Godoy, Valladares & Castro-Díez 2011), mechanisms leading to successful invasion (Callaway & Aschehoug 2000; Keane & Crawley 2002; Callaway & Ridenour, 2004; Blumenthal 2005; Theoharides & Dukes 2007) and impacts of invasive plant species (Lake & Leishman, 2004; Hejda, Pyšek & Jarošík 2009; Pyšek *et al.* 2012; Simberloff *et al.* 2013). Richardson *et al.* (2000) conceptualized the processes along the introduction–naturalization–invasion continuum as a series of filters through which a species must pass. Understanding the ecological and evolutionary processes that underpin a species' ability to move

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along this continuum will substantially increase our ability to predict the likelihood of invasion success and consequent impact (Richardson & Pyšek 2012; Colautti *et al.* 2014).

Significant progress has been made in understanding the role of traits in determining why some introduced species are more successful than others as invaders and also in understanding differences between invaders and co-occurring native species. In particular, a range of studies have shown that successful invaders tend to have traits associated with the capacity for fast growth, such as high specific leaf area (SLA), photosynthetic capacity (A_{max}) and foliar nitrogen (%N; Baruch & Goldstein, 1999; Durand & Goldstein, 2001; Grotkopp, Rejmánek & Rost 2002; McDowell, 2002; Craine & Lee, 2003; Gulias *et al.*, 2003; Leishman *et al.*, 2007; Leishman, Thomson & Cooke, 2010; Osunkoya *et al.*, 2010; Penuelas *et al.*, 2010). Such traits are pivotal to the carbon-capture strategy of a species, where species with high SLA, A_{max}, dark respiration rate (R_d) and %N are at the fast-growth end of the leaf economic spectrum (Wright *et al.* 2004), reflecting a fast return on carbon investment and a capacity for rapid growth when resources are not limiting. Earlier work suggested that although invasive exotic species tend to have traits associated with a fast-growth strategy, these trait combinations do not reflect fundamentally different carbon-capture strategies to those of co-occurring native species (Leishman *et al.*, 2007; Leishman, Thomson & Cooke, 2010, but see Gulias *et al.*, 2003; Funk & Vitousek, 2007).

To understand the mechanisms that mediate movement of species along the introduction–naturalization–invasion continuum, we need to understand how the roles of pre-adaptation and adaptation in the novel environment result in successful naturalization and invasion (Richardson & Pyšek 2012). By 'pre-adaptation' we mean that there is no difference in trait values or ecological strategies between a species' native and introduced ranges, that is, the species' traits provide a successful strategy in both the native and introduced ranges. Note that phenotypic plasticity can be considered a trait, and thus, a shift in trait values between the native and introduced range of a species may reflect a phenotypic response. Recognition of traits that confer invasive capacity prior to a species' introduction to a new location is a key component of weed risk assessment schemes (Groves, Panetta & Virtue 2001). Adaptation implies genotypic responses to selection in the new environment resulting in increased fitness and is also seen as shifts in trait values between the native and introduced ranges. Selection may occur due to specific environmental conditions of the site (e.g. climate, nutrient availability) or due to more generic changes associated with being in a novel environment, such as release from pests and pathogens (Keane & Crawley 2002). It is of course entirely possible that a species introduced to a novel environment may transition along the introduction– naturalization–invasion continuum due to a combination of pre-adaptation and adaptation, that is, the species' traits may be generally suitable to the new environment (pre-adapted) but may be fine-tuned by adaptation to the new conditions. One of the key early hypotheses of the plant invasion literature (the Evolution of Increased Competitive Ability hypothesis – Blossey & Notzold, 1995) predicts evolutionary responses seen as shifts from defensive to growth traits due to release from natural enemies in novel environments. Alternatively, shifts in traits between native and introduced ranges may arise from expression of novel gene combinations due to admixture or hybridization or arise from genetic drift including founder effects (Prentis *et al.* 2008; Whitney & Gabler 2008). Even with low genetic diversity, there is potential for adaptive evolution from founding populations (Dlugosch & Parker, 2008). A review by Whitney & Gabler (2008) provides examples of rapid evolutionary changes in a range of invasive plant species.

Comparative studies of invasive species in their native and introduced ranges are still relatively uncommon and represent an enormous research opportunity (Hierro *et al.*, 2005). Field evidence suggests that reduced herbivory, larger plant size and greater reproductive output are common in introduced plant populations (Crawley, 1986; Hinz & Schwarzlaender 2004; Jakobs *et al.*, 2004; Bossdorf *et al.* 2005; Carpenter & Cappuccino 2005; Hierro *et al.*, 2005; Erfmeier & Bruelheide 2010; Herrera *et al.*, 2011), although there are a number of counter examples (e.g. Franks *et al.*, 2008, Cripps *et al.*, 2010). Common garden experiments allow direct testing of whether trait shifts observed in the field are due to phenotypic or genetic variation. These experiments are often limited in the number of species or populations tested, and so far, results have been equivocal. Thus, the generality of enemy release and trait shifts as important determinants of invasive success in plants introduced to novel regions remains unclear.

In this study, we looked for evidence of release from herbivory and shifts in leaf-level traits between the native and introduced ranges of 13 invasive plant species. We chose species that had been introduced to multiple regions in order to assess whether any trait shifts identified were consistent across different regions in the exotic range. We considered that consistency in the direction of trait shifts across different regions was evidence of selection in response to the general conditions associated with introduction to a novel environment (e.g. enemy release). In contrast, we considered that differences between regions in the direction of any trait shifts identified were evidence for selection in response to particular environmental drivers and/or could have arisen through the interaction of environmental factors and novel gene combinations or by founder effects (genetic drift).

Materials and methods

SPECIES SELECTION, SAMPLING PROTOCOL AND DATA COLLECTION

We selected 13 plant species for this study. The criteria for species selection were that each species had a relatively limited native range in either the Western Cape of South Africa (SA), south-western Australia (WA) or south-eastern Australia (EA), and an exotic range in at least one of the other regions or in the North Island of New Zealand (NZ; see Table 1). We required a relatively limited native range so that we could sample widely across the entire range of the species,

Table 1. Description of species and details of populations sampled. Family and growth form for each of the species is listed and numbers indicate number of populations sampled in each region (SA, South Africa; WA, Western Australia; EA, Eastern Australia; NZ, New Zealand), as well as the total number of populations sampled in the native and exotic ranges. A total of five individuals in each of the 256 populations were sampled

Native range	Species	Family	Growth form	SA	WA	EA	NZ	Native range	Exotic range	Total
South Africa	*Asparagus asparagoides* (L.) Druce	Asparagaceae	Climber	5	5	9	4	5	18	23
	Chrysanthemoides monilifera (L.) Norl. subsp. *monilifera*	Asteraceae	Shrub	5	3	5	5	5	13	18
	Melianthus major L.	Melianthaceae	Shrub	6	4	7	3	6	14	20
	Pelargonium capitatum (L.) Aiton	Geraniaceae	Herb	6	10	0	0	6	10	16
	Polygala myrtifolia L.	Polygalaceae	Shrub	6	7	9	4	6	20	26
Eastern Australia	*Acacia longifolia (Andrews) Willd.*	Fabaceae-Mimosoideae	Tall shrub or tree	6	3	7	4	7	13	20
	Leptospermum laevigatum (Gaertn.) F. Muell.	Myrtaceae	Tall shrub or small tree	6	8	7	0	7	14	21
	Pittosporum undulatum Vent.	Pittosporaceae	Tree	6	3	8	0	9	8	17
	Eucalyptus cladocalyx F. Muell.	Myrtaceae	Tree	6	1	7	0	7	7	14
Western Australia	*Acacia cyclops* G. Don	Fabaceae-Mimosoideae	Tall shrub or tree	6	10	4	0	10	10	20
	Acacia saligna (Labill.) H. L. Wendl.	Fabaceae-Mimosoideae	Tall shrub or tree	6	9	5	1	9	12	21
	Paraserianthes lophantha (Willd.) I. C. Nielsen	Fabaceae-Mimosoideae	Tall shrub or tree	5	7	7	6	7	18	25
	Eucalyptus conferruminata (Schauer) Benth.	Myrtaceae	Mallee tree	6	0	9	0	9	6	15

given limited resources. These regions were selected due to the high number of plant species introductions between the regions. All sites sampled were within the same latitude (30–41°S), with the majority within 32–38°S. Sampling was conducted at the following times: SA, May–June 2004; WA, September–October 2005; EA, May–July 2005; NZ, April 2006.

The 13 species were dominated by woody growth forms but covered a range of families (Table 1). Perennial woody species were preferred as they could be sampled at any time of year and were less likely to be affected by seasonal climate. For each species, we sampled at least five populations in the native range and between 1 and 10 populations in each of the introduced regions (minimum of six populations across all exotic regions, range 6–20, Table 1). We attempted to sample across as much of the range of each species in each region as possible and to incorporate the variety of topographic and habitat features within each region. The total number of populations sampled was 256.

For each population at a site, we randomly selected five plants, avoiding plants that showed evidence of mechanical or chemical control. Twenty leaves of varying ages for each individual plant were randomly selected, and the percentage of damage by herbivores and pathogens, including leaf chew, skeletonizing, gall damage, necrosis and mould, was visually estimated. For simplicity, we refer to this as leaf herbivory. A score of mean percent leaf herbivory was calculated for each individual plant. Five young fully expanded healthy leaves were collected from the outer canopy of individual plants and returned to the laboratory to calculate leaf area, leaf mass and SLA (leaf area per unit dry mass). Leaves were scanned using a LiCor LI-3100 Area Meter or CanoScan LiDE35 to obtain leaf area and then dried at 60 °C for at least 48 h before weighing. The dried leaves of individuals were then bulked within populations before being ground to a fine powder and analysed for %N using a LECO CHN-900 analyser.

Measurements for gas exchange were taken on one young, fully expanded sun leaf of each plant. For $R_{d\text{-}mass}$, one 30-cm twig was cut from each individual and kept cool and hydrated during storage in the dark for at least 1 h (maximum 8 h, generally <3 h) before measurements were taken. A_{max} and R_d were measured using a LI-6400 portable photosynthesis system. For A_{max}, measurements were taken in the morning with ambient CO_2 concentration maintained at 390 ppm, a flow rate of 500 μL L^{-1}, Photosynthetically-active radiation PAR at 1500 μmol m^{-2} s^{-1}, relative humidity at 40–70%, stomatal index at 1.00 and block temperature at 20 °C. For R_d, flow was maintained at 200–500 μL L^{-1}, CO_2 reference at 390 ppm, PAR at 0 μmol m^{-2} s^{-1}, relative humidity at 40–70%, stomatal index at 1.00 and leaf temperature at 20 °C. If a single leaf did not fill the chamber, A_{max} and R_d were adjusted for leaf area measured as required. Gas exchange leaves were retained in order to calculate leaf area and dry mass using the method described above. All assimilation and respiration rates were calculated on a per g dry matter basis for analysis.

DATA ANALYSIS

Our data were cross-classified in structure, that is, a population could be in multiple categories (species, region, origin, range), but not in a hierarchical fashion. This prohibited the use of classic ANOVA and general linear mixed models. Hence, we used Markov Chain Monte Carlo general linear mixed model (MCMCglmm) estimation of parameters describing the effect of native vs. invasive range on the traits of species, with a cross-classified structure using Bayesian linear mixed models. This approach supports a range of distributions and diverse variance structures for the random effects and has previously been used to model traits in invasive species (Ruprecht, Fenesi & Nijs 2014). The approach steps through parameter combinations, such that given enough iterations, the probability of a parameter combination appearing in the chain is proportional to its posterior probability. We

applied the analyses with a non-informative prior using logged data. We used 13 000 iterations with the first 3000 'burn-in' iterations discarded. The mean of each parameter was calculated, as was the 2.5th and 97.5th percentiles of the samples. These percentiles were used to describe the 95% Bayesian credible interval. Two models were run for each plant trait. In the first model, we considered the range (native vs. exotic) of each plant, with origin (EA, WA, SA), region in which measurements were made, species and population as random factors. For the analysis of nitrogen concentration, the population term was not included as data were population means. In the second model for each trait, we considered the interaction between range and origin to account for the possibility that invasive species from some origins had different trait responses to species from other origins. Deviance information criterion (DIC) values were used to evaluate if the second model better described the data. Unless the DIC value of the more complex model was lower by >5, the simpler model was considered best (Bolker 2008). For all seven plant traits, the DIC value for the more complicated model did not differ by more than two; hence, only the results of the simpler model are presented.

For factors and traits that were found to be significant using the MCMCglmm analysis, we conducted further analyses at the species level in order to identify trait shifts within species between native and introduced ranges and between regions. We used linear mixed models to test for differences in leaf traits between each species' native and introduced range with range treated as a fixed factor (native, exotic) and region (SA, WA, EA, NZ) as a random factor, with population nested within region. To test for differences between regions, linear mixed models were used with region (SA, WA, EA, NZ) as a fixed factor and population as a random factor. Pairwise comparisons between regions were made using *t*-tests with pooled variance and corrected using a Bonferroni adjustment.

All traits were $\log_{10}$-transformed when necessary to conform to assumptions of normality. Data analysis was conducted using the nlme (Pinheiro *et al.* 2012) and mcmc (Geyer & Johnson 2013) packages in R (R Core Team 2014).

Results

The most parsimonious MCMCglmms were those with range as the fixed factor, and none of the models for any of the response variables were improved by including an interaction between range and origin, suggesting that species' responses to introduction to a new range are independent of origin. MCMCglmm analyses showed that across all species leaf herbivory was significantly different between native and exotic ranges (Table 2), with percent leaf damage lower in the exotic compared to native ranges (Fig. 1). Species' range (native vs. exotic) was also a significant factor explaining variation in two of the six leaf-level traits measured. Both SLA and leaf area were larger in exotic compared to native ranges (Table 2, Fig. 1), but there were no significant differences in leaf mass, A_{mass}, $R_{d\text{-}mass}$ or % N between ranges.

We then examined differences between ranges and regions at the species level for the three factors found to be significantly different across all species. Leaf herbivory was significantly reduced compared to the native range in at least 1 exotic region for eight of the 13 species, and no regions within the exotic range showed higher rates of leaf herbivory (Table 3 and Fig. 1). For three of the species, leaf herbivory was significantly lower in all exotic regions examined (three regions – *Asparagus asparagoides, Chrysanthemoides monilifera*, one region *Pelargonium capitatum*). For *C. monilifera*, the reduced leaf herbivory in all exotic regions resulted in an overall significant difference between the native and exotic range ($P = 0.029$, Table 3). Leaf herbivory was significantly lower in two out of three exotic regions for three species (*Melianthus major*, *Acacia cyclops*, *Acacia saligna*) and in one region only for *Eucalyptus cladocalyx* and *Pittosporum undulatum*.

Species- and region-level analysis of SLA showed that six of the 13 species had significantly greater SLA in at least one of the exotic range regions compared to its native range while only one species (*Paraserianthes lophantha*) had a significantly smaller SLA and that was in only one out of the three exotic regions examined (Table 4, Fig. 1). Of the six species which had a significant shift to greater SLA in the exotic range, two species showed the shift in all regions examined (three regions – *C. monilifera*; one region *P. capitatum*), two species in two out of three regions (*A. asparagoides*, *Polygala myrtifolia*) and two species in one out of three regions (*M. major, E. cladocalyx*). For *C. monilifera*, the higher values of SLA in each of the three exotic regions resulted in an overall significant difference between its native and exotic range ($P = 0.04$, Table 4).

Table 2. Estimates of the posterior model (β) and 95% credible intervals (95% CI) for fixed factor contrasts. Parameter estimates whose 95% CI did not cross zero were considered statistically significant. As more complicated models, which included an interaction between range and region, had deviance information criterion (DIC) values that differed little from the simpler model, only the simple model parameters are shown, but the DIC values of both models are provided. Significant results are shown in bold

Trait	Native posterior mean	Native 95% CI	Exotic posterior mean	Exotic 95% CI	pMCMC	DIC	DIC of more complex model
Herbivory %	0.048	0.034–0.062	0.190	0.140–0.244	**<0.001**	−84.3	−85.9
SLA	0.955	0.78–1.14	−0.056	−0.082 to −0.029	**<0.001**	−2527.9	−2528.8
Leaf Area	3.02334	2.689–2.206	−0.089	−0.129 to −0.051	**<0.001**	−2007.2	−2007.6
Leaf Mass	−0.955	−1.303 to −0.594	0.012	−0.352 to 0.059	0.586	−1460.3	−1460.4
A_{mass}	−1.026	−1.224 to −0.823	−0.049	−0.107 to 0.018	0.124	−604.3	603.7
$R_{d\text{-}mass}$	−2.127	−2.300 to −1.981	−0.009	−0.051 to 0.047	0.758	−669.446	−668.30
%N	−2.204064	−2.423 to −1.998	−0.006	−0.080 to 0.063	0.898	108.25	108.15

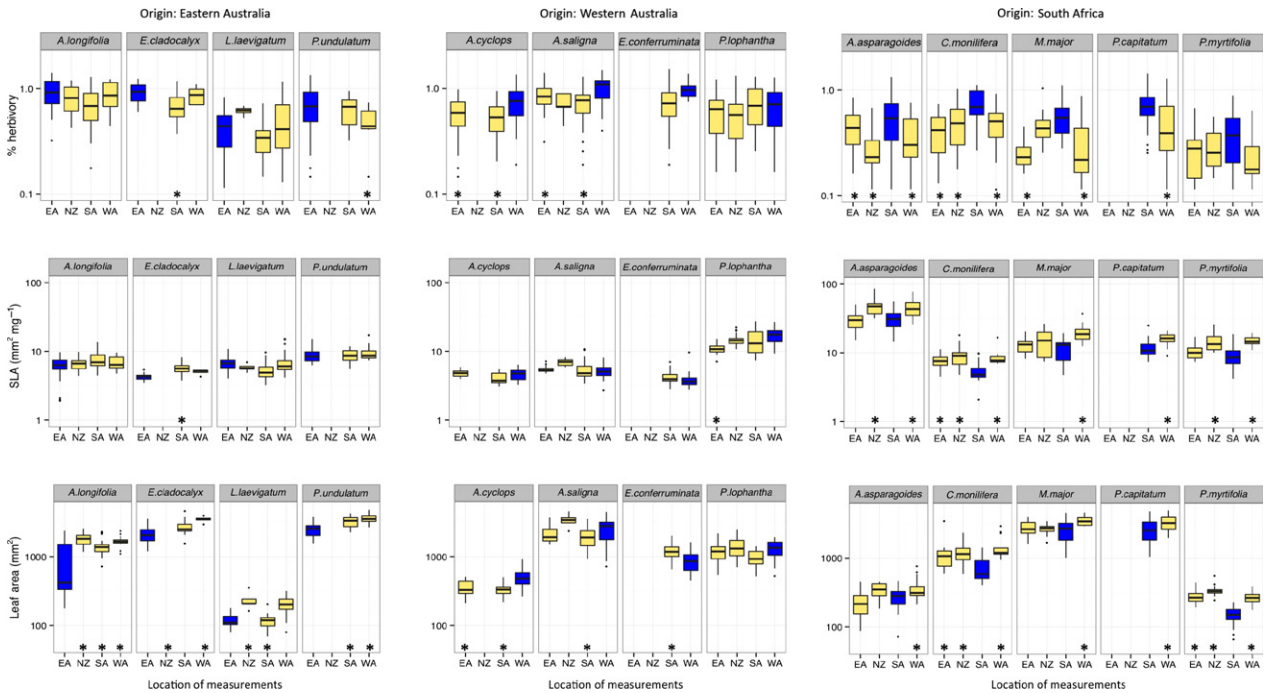

Fig. 1. Boxplot showing leaf herbivory (top row), specific leaf area (SLA; middle row) and individual leaf area (bottom row) in the native and exotic ranges of 13 invasive plant species. Boxes represent 25–75% of the data with whiskers extending from 5% to 95%. Within boxes, solid lines indicate medians. Blue boxes show data collected in the native range and yellow boxes are from the exotic ranges. The asterisks identify regions in which trait values were significantly different to values from their native region. The left-hand cluster of columns shows species originating from Eastern Australia, the middle cluster shows species from Western Australia, and the right-hand cluster shows species from South Africa. SA, South Africa; WA, Western Australia; EA, Eastern Australia; NZ, New Zealand.

Table 3. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA, South Africa; WA, Western Australia; EA, Eastern Australia; NZ, New Zealand) on leaf herbivory. Arrows indicate the direction of a shift in value compared to the native range when the difference was significant at $P < 0.05$ (shown in bold). Significance values <0.10 are shown. The dash (–) indicates no data

		Effect of range			Effect of region			Region *post hoc* comparisons			
Native range	Species	d.f.	*F*	*P*	d.f.	*F*	*P*	SA	WA	EA	NZ
South Africa	*Asparagus asparagoides*	1,2	15.5	0.058	3,19	5.61	**0.006**	Native	**0.006** ↓	**<0.001** ↓	**<0.001** ↓
	Chrysanthemoides monilifera subsp. *monilifera*	1,2	32.67	**0.029** ↓	3,14	12.17	**<0.001**	Native	**0.002** ↓	**<0.001** ↓	**<0.001** ↓
	Melianthus major	1,2	5.52	0.143	3,16	6.66	**0.004**	Native	**<0.001** ↓	**<0.001** ↓	ns
	Pelargonium capitatum	–	–	–	1,12	3.17	**0.003**	Native	**0.001** ↓	–	–
	Polygala myrtifolia	1,2	4.49	0.168	3,21	2.35	0.101	Native	ns	ns	ns
Western Australia	*Acacia cyclops*	1,2	17.12	0.15	2,17	8.58	**0.026**	ns	Native	**0.016** ↓	**<0.001** ↓
	Acacia saligna	1,2	8.93	0.096	3,17	3.396	**0.042**	**<0.001** ↓	Native	**0.045** ↓	ns
	Paraserianthes lophantha	1,2	0.152	0.733	3,21	0.491	0.692	ns	Native	ns	ns
	Eucalyptus conferruminata	–	–	–	1,13	2.20	0.16	ns	Native	–	–
Eastern Australia	*Acacia longifolia*	1,2	2.11	0.2831	3,15	1.09	0.380	ns	ns	Native	ns
	Eucalyptus cladocalyx	1,1	12.07	0.17	2,11	7.84	**0.007**	**<0.001** ↓	ns	Native	–
	Leptospermum laevigatum	1,2	0.179	0.713	3,17	1.84	0.178	ns	ns	Native	ns
	Pittosporum undulatum	1,2	3.44	0.31	2,12	2.33	**0.05**	ns	**0.014** ↓	Native	ns

The shifts to greater SLA in regions within the exotic range were largely due to shifts to larger leaf area rather than to smaller leaf mass. Leaf area was consistently larger across species in regions within the exotic range. Ten out of 13 species had significantly larger leaf area in at least one of the regions within its exotic range while only two species had reduced leaf area in an exotic range region (Table 5 and Fig. 1). Six species had a shift to larger leaf area in all regions examined (three regions – *C. monilifera*, *P. myrtifolia, Acacia longifolia*; two regions – *P. undulatum*; one region *P. capitatum; Eucalyptus conferruminata*), three species in two out of three exotic regions (*E. cladocalyx*, *Leptospermum laevigatum, P. undulatum*) and one species in one out of three exotic regions (*A. asparagoides*). For *P. myrtifolia*,

Table 4. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA, South Africa; WA, Western Australia; EA, Eastern Australia; NZ, New Zealand) on specific leaf area. Arrows indicate the direction of a shift in value compared to the native range when the difference was significant at $P < 0.05$ (shown in bold). Significance values <0.10 are shown. The dash (–) indicates no data

		Effect of range			Effect of region			Region *post hoc* comparisons			
Native range	Species	d.f.	*F*	*P*	d.f.	*F*	*P*	SA	WA	EA	NZ
South Africa	*Asparagus asparagoides*	1,2	0.88	0.44	3,19	7.05	**0.002**	Native	**<0.001** ↑	ns	**<0.001** ↑
	Chrysanthemoides monilifera subsp. *monilifera*	1,2	20.02	**0.04**	3,14	8.67	**0.002**	Native	**<0.001** ↑	**0.004** ↑	**<0.001** ↑
	Melianthus major	1,2	2.07	0.286	3,16	4.70	**0.015**	Native	**<0.001** ↑	ns	ns
	Pelargonium capitatum	–	–	–	1,12	11.72	**0.005**	Native	**<0.001**↑	–	–
	Polygala myrtifolia	1,2	4.498	0.168	3,21	10.07	**<0.001**	Native	**<0.001** ↑	ns	**<0.001** ↑
Western Australia	*Acacia cyclops*	1,7	0.77	0.53	2,17	1.73	0.206	ns	Native	ns	–
	Acacia saligna	1,2	1.308	0.37	3,16	1.248	0.325	ns	Native	ns	ns
	Paraserianthes lophantha	1,2	4.180	0.177	3,21	5.244	**0.007**	ns	Native	**<0.001** ↓	ns
	Eucalyptus conferruminata	–	–	–	1,13	2.59	0.13	ns	Native	–	–
Eastern Australia	*Acacia longifolia*	1,2	2.23	0.273	3,14	1.27	0.322	ns	ns	Native	ns
	Eucalyptus cladocalyx	1,1	29.5	0.115	2,11	17.78	**<0.001**	**<0.001** ↑	0.10	Native	–
	Leptospermum laevigatum	1,2	0.25	0.66	3,17	0.957	0.435	ns	ns	Native	ns
	Pittosporum undulatum	1,1	0.27	0.69	2,13	0.52	0.60	ns	ns	Native	–

Table 5. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA, South Africa; WA, Western Australia; EA, Eastern Australia; NZ, New Zealand) on leaf area, where leaf area represents the area of an individual leaf. Arrows indicate the direction of a shift in value compared to the native range when the difference was significant at $P < 0.05$ (shown in bold). Significance values <0.10 are shown. The dash (–) indicates no data

		Effect of range			Effect of region			Region *post hoc* comparisons			
Native range	Species	d.f.	*F*	*P*	d.f.	*F*	*P*	SA	WA	EA	NZ
South Africa	*Asparagus asparagoides*	1,2	0.14	0.74	3,19	4.566	**0.014**	Native	**0.034** ↑	0.07	ns
	Chrysanthemoides monilifera subsp. *monilifera*	1,2	11.45	0.07	3,14	5.47	**0.012**	Native	**<0.001** ↑	**0.020** ↑	**0.030** ↑
	Melianthus major	1,2	0.039	0.861	3,16	6.247	**0.005**	Native	**<0.001** ↑	ns	ns
	Pelargonium capitatum	–	–	–	1,12	2.56	**<0.001**	Native	**0.005** ↑	–	–
	Polygala myrtifolia	1,2	56.44	**0.017** ↑	3,21	25.029	**<0.001**	Native	**<0.001** ↑	**<0.001** ↑	**<0.001** ↑
Western Australia	*Acacia cyclops*	1,1	21.04	0.136	2,17	10.54	**0.001**	**<0.001** ↓	Native	**<0.001** ↓	ns
	Acacia saligna	1,2	4.01	0.183	3,16	1.18	0.185	ns	Native	ns	ns
	Paraserianthes lophantha	1,2	0.337	0.62	3,21	2.14	**0.048**	**0.004** ↓	Native	ns	ns
	Eucalyptus conferruminata	–	–	–	1,13	6.122	**0.027**	**<0.001** ↑	Native	–	–
Eastern Australia	*Acacia longifolia*	1,2	16.14	0.06	3,14	7.44	**0.003**	**<0.001** ↑	**<0.001** ↑	Native	**<0.001** ↑
	Eucalyptus cladocalyx	1,1	9.622	0.198	2,11	7.03	**0.01**	**<0.001** ↑	**<0.001** ↑	Native	ns
	Leptospermum laevigatum	1,2	1.668	0.3256	3,17	22.50	**<0.001**	ns	**<0.001** ↑	Native	**<0.001** ↑
	Pittosporum undulatum	1,2	13.77	0.16	2,14	7.17	**0.007**	**<0.001** ↑	**<0.001** ↑	Native	–

consistently larger leaf area in exotic regions resulted in a significant overall difference between the native and exotic range ($P = 0.017$, Table 5), and for two other species (*C. monilifera* and *A. longifolia*), there was a marginally significant greater leaf area in the exotic range ($P = 0.07$, 0.06 respectively, Table 5). In contrast, leaf mass was smaller in at least one exotic region for three species (*A. asparagoides, A. saligna, A. longifolia*) and larger for four species (*P. myrtifolia, P. lophantha, L. laevigatum* and *P. undulatum*; S1). Table 6 summarizes the trait shifts across species and shows clearly that increases in SLA in exotic range regions are consistently associated with increases in leaf area.

We then assessed the evidence for whether reductions in leaf herbivory resulted in shifts to traits associated with faster growth in the exotic range within species. The data in Table 6 show that reduced leaf herbivory in the native range is associated with increases in SLA and leaf area within species consistently across exotic regions (six out of eight species that had reduced leaf herbivory in exotic regions also had increased SLA or leaf area in those regions). Five of the six species that had reduced herbivory in the native range had significant increases in SLA and leaf area (*A. asparagoides, C. monilifera, M. major, P. capitatum, E. cladocalyx*), while *P. undulatum* had an increase in leaf area only. We also tested whether herbivory was negatively correlated with SLA, leaf area and %N within populations and within species. Within-species relationships were generally non-significant (Table S1 in Supporting Information) and inconsistent in direction (Fig. S1 in Supporting Information).

Table 6. Summary of results showing significant differences ($P < 0.05$) between the native range and each exotic region (SA, South Africa; WA, Western Australia; EA, Eastern Australia; NZ, New Zealand) for leaf herbivory and six leaf-level traits (SLA specific leaf area, LA leaf area, LM leaf mass, A_{mass} assimilation rate, $R_{d\text{-}mass}$ dark respiration, %N foliar nitrogen). Arrows indicate the direction of the shift in exotic region values compared to the native range (decrease ↓, increase ↑)

Native range	Species	Herbivory	SLA	LA	LM	A_{mass}	$R_{d\text{-}mass}$	%N
South Africa	*Asparagus asparagoides*	↓ WA, EA, NZ	↑ WA, NZ	↑ WA	↓ EA	↑ NZ		
	Chrysanthemoides monilifera subsp. *monilifera*	↓ WA, EA, NZ	↑ WA, EA, NZ	↑ WA, EA, NZ		↑ WA, NZ	↑ WA, EA, NZ	↑ WA, EA, NZ
	Melianthus major	↓ WA, EA	↑ WA	↑ WA		↑ WA	↑ WA, EA	↓ EA, NZ
	Pelargonium capitatum	↓ WA	↑ WA	↑ WA				↓WA
	Polygala myrtifolia		↑ WA	↑ WA, EA, NZ	↑ EA, NZ			↓WA
Western Australia	*Acacia cyclops*	↓ EA, NZ		↓ SA, EA		↓ SA		↓ SA, EA
	Acacia saligna	↓ SA, EA			↓ SA, EA, NZ	↑ EA, NZ		
	Paraserianthes lophantha		↓ EA	↓ SA	↑ EA, NZ	↓ SA, EA	↓ SA, EA, NZ	↓ SA, EA, NZ
	Eucalyptus conferruminata			↑ SA			↑ SA	↑ SA
Effect of region	*Acacia longifolia*			↑ SA, WA, NZ	↓ SA	↑ WA, NZ		↑ NZ
	Eucalyptus cladocalyx	↓ SA	↑ SA	↑ SA, WA		↑ SA		
	Leptospermum laevigatum			↑ WA, NZ	↑ WA, NZ		↓WA	
	Pittosporum undulatum	↓WA		↑ SA, WA	↑ SA, WA		↓ SA	↓ SA

Results of the species- and region-level analyses for the traits that were found not to be significantly different overall between the native and exotic ranges are presented in Supplementary Material (Tables S2–S5).

Discussion

We examined evidence for reduced herbivory and differences in leaf-level traits associated with a shift to a faster growth strategy in multiple exotic range regions compared to the native range for 13 invasive plant species. By looking across multiple regions and multiple species, we were able to assess the consistency of any trait shifts identified. We suggested that consistency in the direction of trait shifts across regions and species would provide evidence for either phenotypic (i.e. plasticity) or genetic adaptation in response to introduction to a novel environment while differences between species in trait shift directions would indicate a stronger role of other drivers such as site-specific environmental conditions, genetic drift and novel genetic variation.

We found clear evidence for reduced leaf herbivory in exotic regions compared to the native range consistently across species and for the majority of species studied (Tables 2 and 6). Eight out of 13 species had significantly lower levels of leaf herbivory in exotic range regions. Many previous studies have shown reduced leaf herbivory in exotic compared to native species (e.g. Lake & Leishman, 2004; Carpenter & Cappuccino 2005; Liu & Stiling, 2006; Hill & Kotanen 2010), but there are fewer studies that compare native and exotic range populations, and such studies typically consider only one or a few species (e.g. DeWalt, Denslow & Ickes 2004; Adams *et al.* 2009). Hinz and Schwarzlaender (2004) reviewed results from a range of studies and showed that herbivory was typically reduced in exotic range populations, associated with a shift to generalist and exophagous species. Bossdorf *et al.* (2005) reviewed studies of 18 species and reported reduced herbivory in the exotic range for eight species. Liu and Stiling (2006) showed in a meta-analysis that herbivore damage was only slightly reduced in exotic compared to native range populations within species, most likely due to the low number of studies. Our study has provided additional evidence for reduced herbivory in exotic range populations consistently across a range of species.

Some studies have suggested a direct causal link between reduced herbivory in the exotic range and increased plant growth and reproductive output (e.g. Ebeling, Hensen & Auge 2008), while other studies have found reduced herbivory but no evidence of increased growth (e.g. Cripps *et al.*, 2010). The enemy release hypothesis (Keane & Crawley 2002) suggests that release from top-down control by pests and pathogens may result in increased individual growth and a consequent increase in population size and abundance, allowing invasive spread. Although Maron & Vilà (2001) suggested that top-down herbivore effects are likely to be strongest on annual plants, we found clear evidence of release from herbivore pressure across our sample of largely woody

perennial species, with a reduction in leaf herbivory in the exotic range resulting in a shift in leaf-level trait values, consistent with a shift to a faster growth strategy. We found consistent shifts to higher values of leaf area and SLA across species and exotic regions. There was also evidence of consistent shifts among species to larger A_{mass} in exotic regions (six of 13 species had larger A_{mass} in at least one region within the exotic range compared with only two species with smaller A_{mass}, Table S1), but this was not significant across all species (Table 2). Of the eight species that had reduced herbivory in their exotic range, six showed shifts to significantly larger SLA or leaf area (Table 6). Only two species (*A. saligna and A. cyclops*) had a significant reduction in leaf herbivory in their exotic range but no increase in SLA or leaf area. In a related study comparing growth and seed production in native and exotic ranges within Australia, Harris *et al.* (C.J. Harris, B.R. Murray, A.T. Moles & M.R. Leishman, unpubl. data) showed that *A. longifolia* grew significantly larger and produced more seeds per unit canopy area in its exotic range in Western Australia compared to its native range in Eastern Australia. Some of our study species that had non-significant reductions in leaf herbivory (*P. myrtifolia, E. conferruminata, A. longifolia, L. laevigatum*) also showed shifts to trait values associated with faster growth strategies in exotic regions. It is important to note that the percentage of leaf damaged by herbivores is only one simple measure of enemy release, and it is quite possible that the abundance of other pests (e.g. stem borers, root herbivores, seed predators) and pathogens was reduced in the exotic range for any of the 13 species studied.

The increases in SLA found in six of the 13 species were underpinned by increases in leaf area, rather than decreases in leaf mass. Why might reduced pressure from leaf herbivores result in larger leaf size? Moles & Westoby (2000) showed in a comparative study of 51 species that leaf size was positively correlated with leaf expansion time. They suggested that as leaves are most vulnerable to herbivores during deployment and expansion, high levels of herbivory may result in selection pressure for smaller leaves. Thus, it seems likely that plants introduced into a novel range that experience relatively low levels of herbivory may have less constraint on their leaf size, resulting in a shift to larger leaves and subsequently larger SLA (when leaf mass is not increased concurrently).

In earlier studies, we showed that species in their exotic range had a suite of leaf-level traits associated with fast growth, while in comparison native co-occurring species tended to be placed at the slow-growth end of the leaf economic spectrum (Leishman *et al.*, 2007; Leishman, Thomson & Cooke, 2010). In order to understand how species introduced into a novel range are able to move along the introduction–naturalization–invasion continuum (*sensu* Richardson *et al.* 2000; Colautti *et al.* 2014), it is important to understand whether plants in their exotic range are successful due to pre-adaptation (i.e. their native range functional traits including phenotypic plasticity), adaptation under selection to different environmental conditions, genetic drift or expression of novel gene combinations due to admixture or hybridization. Colautti *et al.* (2014) used occurrence data of 1416 species to assess the relative importance of pre-adaptation compared to extrinsic ecological and genetic factors in determining invasiveness. They found support for both mechanisms but concluded that invasiveness was better explained by interspecific variation in invasion potential than by biogeographical changes in performance. In this study, we showed that in all of the 13 study species there were significant leaf-level trait differences between the native range and regions in the exotic range, with 11 of the 13 species showing trait differences consistent with a shift to a faster growth strategy. This suggests that plants introduced to a new environment are remarkably adaptable, due to phenotypic plasticity and/or genotypic adaptation. This is consistent with observations that many invasive species are much more common and abundant in their exotic compared to their native range (see review in Hierro *et al.*, 2005 and Parker *et al.* 2013 but see Firn *et al.* 2011) and that many species are able to occupy different climate niches or biomes in their new range (Gallagher *et al.* 2010; but see Petitpierre *et al.* 2012).

If species were successful in their exotic range due to phenotypic plasticity (e.g. Davidson, Jennions & Nicotra 2011) or adaptation due to selection in response to particular environmental conditions, we might expect to see trait differences between the native and exotic ranges, but the direction of these trait differences would vary due to different environmental conditions in the different exotic regions. In this study, we showed that the direction of trait differences between the native and exotic range regions was surprisingly consistent. No species showed differences in the direction of trait shifts from the native range between different exotic regions (Table 6). This suggests that the driver of selection on these traits in the exotic range is consistent across regions and hence is most likely to be associated with a general aspect of novel environments, such as reduced herbivory.

In a related study, Harris *et al.* (2012) examined genetic diversity of five woody Fabaceae species from native and exotic range populations and compared these to traits of the species grown in a common garden experiment. Four of their five species were in common with this study, although one only exotic region (within Australia) was compared with the native range. *Acacia longifolia* had reduced genetic diversity in the exotic range, but seedlings grown from seed collected in the exotic range had larger SLA and greater biomass. *Acacia cyclops* seedlings had larger relative growth rate, while *A. saligna* and *P. lophantha* showed reduced genetic diversity in the exotic range but no trait differences. These findings suggest that the increases in leaf area and A_{mass} for *A. longifolia* in Western Australia observed in the current study may be attributable to evolutionary adaptation rather than simply phenotypic plasticity. An alternative explanation is that provenances with fast growth were selected for by land managers when the species was introduced for rehabilitation purposes.

How likely is it that the shifts to higher values of the leaf-level traits observed in exotic regions would translate to faster growth, greater biomass or increased reproductive output? The leaf economic spectrum describes a suite of traits that underpin a species' growth strategy (Wright *et al.* 2004)

including SLA, A_{mass}, $R_{d\text{-}mass}$, %N and leaf longevity. It is clear that the trait shifts observed in this study are generally consistent across some of these traits (i.e. leaf area and SLA across all species, A_{mass} for some species), but not others (% N, $R_{d\text{-}mass}$). SLA and A_{mass} are strong drivers of plant relative growth rate (Porter & Remkes 1990; Shipley 2006), and so it is likely that increases in the value of these traits in the exotic range would result in faster growth and greater biomass if light and soil resources were sufficient. Other work from our laboratory (C. Harris & M. Leishman, unpubl. data) has shown that for two of the species in our study (*A. longifolia* and *P. lophantha*), individuals in their Australian exotic range were larger and/or had greater seed production. The variation in %N shifts between native and exotic regions seen across species may reflect differences in soil nutrient conditions; however, the direction of differences between native and exotic regions within each species was surprisingly consistent. Overall, the percentage shift in SLA and A_{mass} between native and exotic regions averaged 49% (SLA) and 41% (A_{mass}). This represents a substantial increase in individual trait values that would be likely to result in increased plant growth, particularly if associated with increases in other leaf-level traits that drive growth rates.

This study has provided clear evidence of reduced leaf herbivory in exotic regions consistently across a range of species and evidence of shifts to higher values of SLA and leaf area consistently across exotic regions and species. These results provide evidence that introduction of a species into a novel environment often results in a reduction in the top-down constraint imposed by herbivores on plant growth, allowing plants to shift towards a faster growth strategy, which may result in an increase in population size and spread and consequently to invasive success. This study has broader implications for our understanding of ecological communities and our assessment of weed risk. Firstly, the results suggest that the role of top-down effects of pests and pathogens in controlling populations may be more influential than previously thought. This suggests that biological control methods are likely to be successful for many alien invasive plant species. Secondly, the consistent differences in traits seen between native and exotic ranges suggest that plants are remarkably adaptable and may be less constrained by novel environments than previously thought. Finally, the results suggest that weed risk assessment systems should explicitly incorporate the adaptive capacity of plant species, as determined by phenotypic plasticity, environmental niche breadth and genetic diversity, in addition to the trait values of species observed in the native range.

Acknowledgements

We thank the many people who provided invaluable assistance in the field, including Karen Alston, Alex Schultz, Brian Cooke, Tatjana Schmidt and Marisa Nordenstahl. Many people also assisted in other ways, including Richard Hobbs, Rachel Standish, Tatjana Schmidt, Alex Schutz, Nicole Vella, Garreth Kyle, Claire Keatley, Barb Rice, Nan Lloyd and Lawrie Twigg. We thank the following institutions for providing support or access: Kirstenbosch Botanical Gardens, University of Cape Town's Botany Department, Department of Environment and Sustainability Victoria, NSW National Parks & Wildlife Service, Department of Environment and Heritage South Australia, Conservation and Land Management Western Australia, Western Australia Main Roads, Department of Conservation New Zealand. This research was funded through an Australian Research Council Discovery grant to ML and DR. DR acknowledges support from the DST-NRF Centre of Excellence for Invasion Biology, the South African National Research Foundation (Grant 85417) and the Hans Sigrist Foundation.

Data accessibility

Data from this study are available from the Dryad Digital Repository (Leishman, Cooke & Richardson 2014).

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Received 12 May 2014; accepted 12 August 2014
Handling Editor: Jonathan Newman

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relationship between % herbivory and leaf area or specific leaf area (SLA) for each of the species where a significant relationship was found from GLM analysis across all populations (Table S1).

Table S1. Result of GLM analyses for each of the 13 species to examine the relationship between leaf herbivory and the traits SLA, leaf area & foliar N. Percentage herbivory was included as a fixed factor and population as a random factor.

Table S2. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA South Africa, WA western Australia, EA eastern Australia, NZ New Zealand) on leaf mass.

Table S3. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA South Africa, WA western Australia, EA eastern Australia, NZ New Zealand) on assimilation rate (A_{mass}).

Table S4. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA South Africa, WA western Australia, EA eastern Australia, NZ New Zealand) on dark respiration ($R_{d\text{-}mass}$) Arrows indicate the direction of a shift in value compared to the native range when the difference was significant at $P < 0.05$ (shown in bold).

Table S5. Results of mixed linear model analyses for the effect of range (native, exotic) and region (SA South Africa, WA western Australia, EA eastern Australia, NZ New Zealand) on foliar nitrogen (%N).

